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ANATOMICAL RE-DESCRIPTION OF THE TERRESTRIAL ONCHIDIID SLUG *SEMPERONCIS MONTANA* (PLATE, 1893)

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ABSTRACT

Onchidiidae, one of the higher clades of pulmonates, have been understudied for the last 70 years; its systematics is in a state of confusion; and the internal anatomy of most species is still largely unknown. The anatomy of *Semperoncis montana*, a terrestrial species that lives in high-elevation rain forests of the Philippines Islands, is redescribed based on 91 specimens representing ten populations. New geographic records (Panay Island) and elevation records (up to 1,850 m) are provided. All type material available was re-examined. The intra-specific variation of anatomical characters is analyzed, with special attention to the radula and the male reproductive organs. Male organs (penial stalk and hooks, papillae and spines of accessory glands) are illustrated using scanning electron microscopy for the first time in onchidiids. Ontogenetic changes in the shape of male organs are described and illustrated in detail, indicating that *S. montana* was described based on immature specimens of the later named *Platevindex apoikistes*. Therefore, this latter name is regarded as a junior synonym of *S. montana*. The supra-specific relationships of *S. montana* are commented upon.

Key words: Euthyneura, intra-specific variation, Gastropoda, Philippines, Pulmonata.

INTRODUCTION

Onchidiidae, one of the higher clades of pulmonates, is poorly known, mainly because it has been understudied for the last 70 years and because its systematics has never been revised (Dayrat, 2009). The nomenclatural status of most species names is unknown and onchidiid species diversity is in state of confusion; whether Labbé's (1934) 14 genera refer to monophyletic, paraphyletic, or polyphyletic taxa is unknown; and higher relationships within onchidiids are also unknown. Finally, as Britton (1984) pointed out, virtually nothing is known about the individual variation of the characters used in onchidiid systematics; anatomical knowledge of onchidiids is also poor, the internal anatomy of the vast majority of the species still being unknown. Information on the general morphology of onchidiids, including the terminology traditionally used – such as dorsal eyes, peripodial groove, marginal glands – can be found in Dayrat (2009, and references therein).

Most onchidiid slugs are marine and live in the upper tidal zone, either in rocky, sandy, or muddy habitats, including mangroves. However, two species have been described from brackish habitats and tolerate fresh water: *Onchidium typhae* Buchannan, 1800, and *Labella ajuthiae* (Labbé, 1935). Also, three terrestrial species have been described from high-elevation rainforests: *Semperoncis montana* (Plate, 1893), known from only the three syntypes collected on land (at an unknown elevation) from Sibugan Island, Philippines; *Platevindex ponsonbyi* (Collinge, 1901), known from only the holotype collected at 850–1,060 m from Borneo; and, *Platevindex apoikistes* Tillier, 1983, known from 38 specimens collected from the eastern slope of Mt. Halcon, Mindoro Island, Philippines, at 400–600 m.

The main goal of the present study is to re-evaluate the species diversity of terrestrial onchidiids, that is, more specifically, to determine how many species live on land in the Philippines Islands. It is based on the examination of type material available (*Semperoncis montana* and *Platevindex apoikistes*), as well as 36 new specimens collected from Panay (150–1,850 m) and 14 new specimens from Mindoro (1,200–1,550 m) islands, which represent new geographical (Panay) and elevation records (highest elevation of terrestrial onchidiids previously known was 1,060 m, which is now 1,850 m). Unfortunately, at this stage, the case of *Platevindex ponsonbyi* must be left aside because its type material could not be found, its original description is too short, and no additional material is available (see Discussion).

The present detailed analysis of individual variation suggests that all specimens examined here are members of the same species. Differences previously mentioned between *apoikistes* and *montana* were due to the fact that these two species were described based on sexually mature and immature individuals, respectively. Ontogenetic changes of two key organs for taxonomy – penial apparatus and male accessory gland – are described in detail.

MATERIALS AND METHODS

Material Preparations

In total, 91 specimens were examined for the present study, including 41 types: 38 types (one holotype and 37 paratypes) of *apoikistes*, three syntypes of *montana*, and 50 new, additional specimens. All specimens are deposited in museums: Florida Museum of Natural History, Gainesville (FLMNH), Muséum National d'Histoire Naturelle, Paris (MNHN), and the Naturmuseum Senckenberg, Frankfurt am Main (SMF). The holotype and two paratypes of *apoikistes* were already dissected by Tillier (1983); four additional paratypes were dissected for the present study; the other paratypes were examined externally but not dissected. One syntype of *montana*, dissected prior to the present study, was examined again, including its reproductive organs; the two other syntypes were only examined externally. Finally, out of the 50 new specimens, 27 were dissected and 23 were examined externally.

For the 32 specimens dissected, both the external morphology and the internal anatomy were observed. All anatomical observations were made under a dissecting microscope and drawn with a *camera lucida*. In addition, organs were prepared for scanning electron microscopy (SEM) for most specimens dissected.

Radulae were cleaned in 10% NaOH for a week, rinsed in distilled water for at least a week, briefly cleaned in an ultrasonic water-bath (less than a minute), sputter-coated with gold-palladium, and examined by SEM (UCM SEM-laboratory). Soft parts (penis, penial gland, etc.) were dehydrated in ethanol and critical point dried before coating. In total, 30 SEM stubs were prepared. When a lot included several specimens, each specimen was labeled, both inside the jar and on the stubs, so that future workers will be able to link unambiguously the present anatomical descriptions to particular individuals in museum collections. All SEM stubs prepared for the present study will be sent back with the specimens to the museum collections.

Anatomical Abbreviations

ag	accessory gland
alg	albumen gland
dd	deferent duct
dg	digestive gland
e	esophagus
hd	hermaphroditic duct
hg	hermaphroditic gland
i	intestine
lcg	left cerebral ganglion
rpg	right pleural ganglion
mg	mucous gland
ov	oviduct
pa	papilla (accessory gland)
ps	penial sheath
rcg	right cerebral ganglion
rg	rectal gland
rps	reproductive system
sp	spermatheca
spv	spermoviduct
st	stomach
vg	visceral ganglion

ANATOMICAL RE-DESCRIPTION

Semperoncis Starobogatov, 1976

The type species, by subsequent designation (Starobogatov, 1976: 211): *Semperoncis glabra* (Semper, 1885), *Semperoncis* being a replacement name for *Semperella* Labbé, 1934, *non Semperella* Gray, 1868 (Porifera).

Semperoncis montana (Plate, 1893)
(Figs. 1–75)

Oncis montana Plate, 1893: 194–196, pl. 7, figs. 3, 23; pl. 11, figs. 57, 58, 71; pl. 12, fig. 89. – Hoffmann, 1928: 87–88.

Semperella montana – Labbé, 1934: 236.

Platevindex montana – Tillier, 1983: 198–202, fig. 3.

Platevindex apoikistes Tillier, 1983: 198–202, figs. 1, 2, 4–7, **new synonym.**

Type Material

Three syntypes of *Oncis montana* (SMF 256164): three specimens 18/17 (#1), 15/13 (#2), and 15/15 (#3) mm preserved, leg. Dr. von Möllendorf, [collecting date unknown]. The syntypes of *montana* are in very poor condition as they likely remained dry for a while before being put back in alcohol. As a consequence, they are very rigid and dark brown.

Holotype of *Platevindex apoikistes* (MNHN, no catalogue number): one specimen 40/31 mm preserved, leg. Philippe Bouchet, December 1980; 37 paratypes of *Platevindex apoikistes* (MNHN, no catalogue number): four specimens dissected 35/25 (#1), 23/14 (#2), 42/26 (#3) and 26/14 (#4) mm preserved [other paratypes were not dissected; spm #2 is the smallest paratype, and spm #3 is the largest]. The type material of *apoikistes* is well preserved, both externally and internally; the holotype was entirely dissected and cut in pieces by Tillier for the original description.

Type Localities

Oncis montana: Philippinen, Sibuyan See [Sibuyan Sea], Sibuyan [Island, on land, unknown altitude]. *Platevindex apoikistes*: E slope of Mt. Halcon, Mindoro oriental [Mindoro Island], 400–600 m altitude.

Additional Material Dissected

Philippines, Panay Island, Antique Province, western ridge of Mt. Madja-as, 1,100 m, 6 April 1992, 13 specimens 20/12 (#1), 33/18 (#2), 19/15 (#3), 21/14 (#4), 23/11 (#5) and 32/21 (#6) mm preserved [seven additional specimens were not dissected; spms #1 and #3 are the smallest, and spm #2 is the largest], leg. K. Auffenberg et al., identified as *Onchidium*, [identifier unknown], (FLMNH 245117); Philippines, Panay Island, Antique Province, just below peak Mt. Madja-as, 1,850 m, 8 April 1992, two specimens 28/20 (#1) and 34/19 (#2) mm preserved, leg. PNM staff, identified as *Onchidium*, [identifier unknown], (FLMNH 245142); Philippines, Panay Island, Antique Province, western ridge of Mt. Madja-as, 900 m, 11 April 1992, 14 specimens 32/20 (#1), 25/15 (#2), 23/17 (#3), 32/20 (#4), 28/17 (#5) mm preserved [nine additional specimens were not dissected; spm #2 is the smallest, and spms #1 and #4 are the largest], leg. K. Auffenberg et al., identified as *Onchidium*, [identifier unknown], (FLMNH 245191); Philippines, Panay Island, Capiz Province, 3.0 km NE of Pilar, 150 m, 11°25'24"N, 120°57'44"E, 26 April 1992, 2 specimens 25/19 (#1) and 25/15 (#2) mm preserved, leg. K. Auffenberg et al., identified as *Onchidium*, [identifier unknown], (FLMNH 245549); Philippines, Panay Island, Aklan Province, NE of Mt. Madja-as, 1,430 m, April 1992, 5 specimens 14/9 (#1), 18/12 (#2), 14/10 (#3), 16/9 (#4) and 17/13 (#5) mm preserved, leg. L. Ruedas et al., identified as *Onchidium*, [identifier unknown], (FLMNH 245797).

Philippines, Mindoro Island, Baco Municipality, Mount Halcon, Hanglo, 1,550 m, 4–8 June 1992, one specimen 28/19 mm preserved, leg. Rafe Brown, identified as *Onchidium*, [identifier unknown], (FLMNH 245788); Philippines, Mindoro Island, Mindoro Oriental Province, Baco Municipality, Mount Halcon, N ridge, Dulangan River valley, 1,200 m, 13°17'27"N, 120°59'32"E 27 May 1992, four specimens 26/18 (#1), 23/17 (#2) and 24/23 (#3) mm preserved [a fourth spm 26/22 mm was not dissected], leg. Rafe Brown, identified as *Onchidium*, [identifier unknown], (FLMNH 245776); Philippines, Mindoro Island, Mindoro Oriental Province, Baco Municipality, Mount Halcon, N ridge, Dulangan River valley, 1,200 m, 13°17'27"N, 120°59'32"E, 28 May 1992, nine specimens 35/23 (#1), 25/20 (#2) and 32/28 (#3) mm preserved [six additional specimens were not dissected; spm #1 is the largest, and spm #2 is the smallest], leg. Rafe Brown, identified as *Onchidium*, [identifier unknown], (FLMNH 245777).

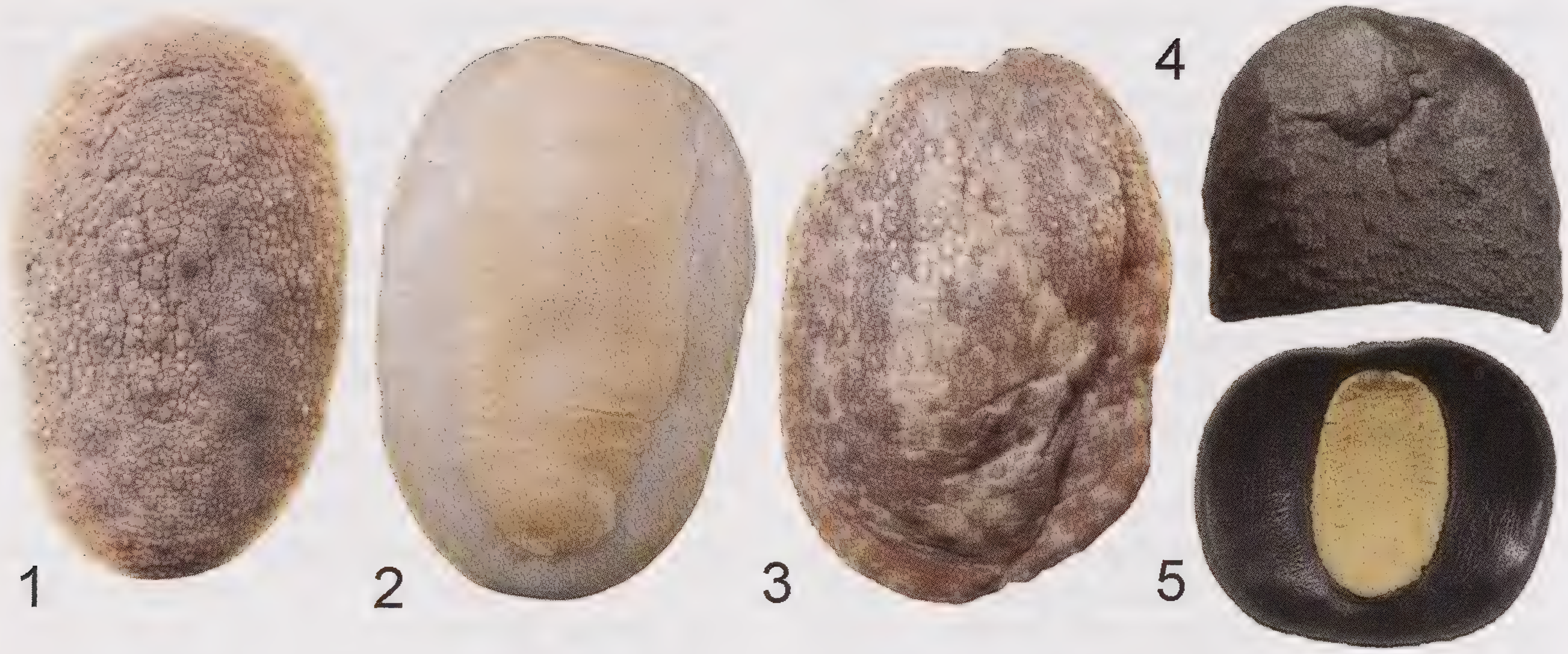
Distribution

Philippines: Sibuyan Island (type locality of *montana*); Panay Island (present study); Mindoro (type locality of *apoikistes*; present study). Note that Hoffmann (1928) and Labbé (1934) cited Plate's (1893) work but did not add new material or data.

From 150 to 1,850 m: 150 m (Panay Isl.), 400–600 m (Mindoro, original description of *apoikistes*), 900 m (Panay Isl.), 1,100 m (Panay Isl.), 1,200 m (Mindoro Isl.), 1,430 m (Panay Isl.), 1,550 m (Mindoro Isl.), 1,850 m (Panay Isl.).

Color (Figs. 1–7)

No information is available on the color of live animals. Dorsal preserved color from light brown mottled with darker areas to homogeneous dark bluish black. Individuals with a dark

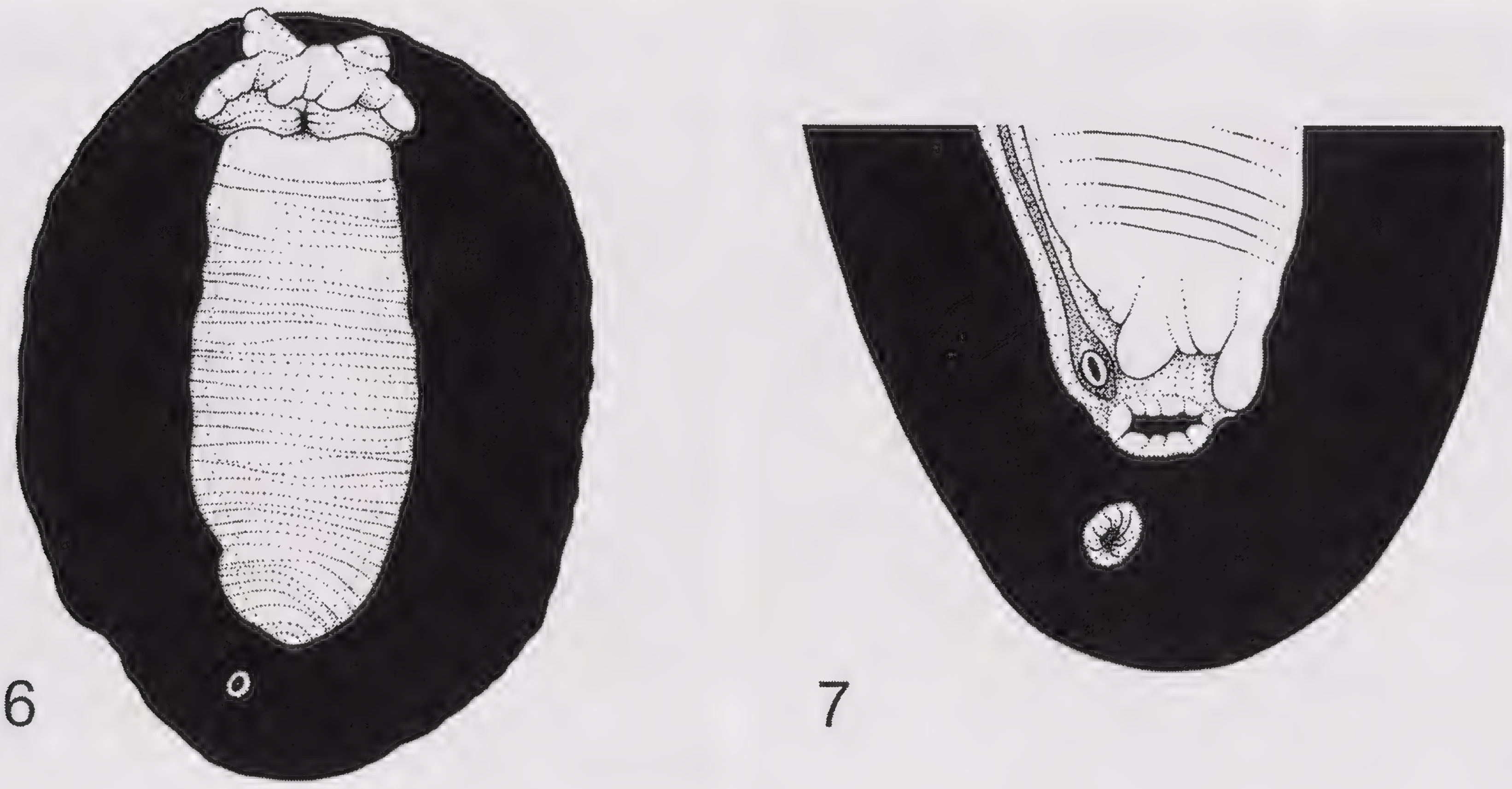


FIGS. 1–5. External morphology and color. FIG. 1: FLMNH 245191 #2, dorsal view, total length = 25 mm; FIG. 2: Same as Fig. 1, ventral view; FIG. 3: FLMNH 245191 #3, dorsal view, total length = 23 mm; FIG. 4: FLMNH 245777, left lateral view, total length of animal (from left to right) = 22 mm; FIG. 5: Same as Fig. 4, ventral view, total length = 22 mm (26 mm in width).

bluish black dorsal notum are found at higher elevation on both Panay (1,850 m, FLMNH 245142) and Mindoro (1,550 m, FLMNH 245788; 1,200 m, FLMNH 245776 & 245777). Populations with a brown dorsal notum are found at lower elevations, from 150 to 1,430 m in Panay, and from 400 to 600 m in Mindoro (type material of *apoikistes*). There is very little individual variation in dark bluish black populations, whereas there is high individual variation in lower-elevation populations: within each lot, the background color varies from light to dark brown mottled with darker areas of varying size and shapes. Finally, the individuals collected at 1,430 m in Panay are, on average, darker than from lower elevations: their color is intermediary between light brown (150–1,100 m) and dark bluish black (1,850 m). The pedal sole is whitish-beige in all specimens. The hyponotum varies from whitish-beige to dark brown; however, all specimens with a dark bluish black dorsal notum have a dark bluish black hyponotum, with or without a lighter margin.

External Morphology (Figs. 1–7)

The notum can be smooth or granular. Most individuals have both granular and smooth portions of notum, depending on how the notum retracted at fixation and preservation. The dorsal notum is oval and, usually longer than wide; some individuals are circular, and, occasionally, individuals may be wider than long. The hyponotum is horizontal. The body is generally flattened, although several individuals are almost conical (e.g., FLMNH 245777 #3, which measures 32/28 mm with a height of 22 mm). Dorsal gills are absent. Papillae with so-called "dorsal eyes" are present in all individuals; the number of papillae varies among individuals (larger individuals may have about 25 of them); all papillae bear one dorsal eye, except for one papilla, located in the center of the notum, which bears three dorsal eyes. The width of the hyponotum relative to the width pedal sole varies among individuals, even within the same lot: for example, within the lot FLMNH 245117, the ventral measurements are 1/16/1 mm (left hyponotum width / sole width / right hyponotum width) for spm #2 and 6/9/6 mm for spm #6. So, to use Labbé's (1934) standard terms, the total width of the hyponotum (left and right sides added) can be superior (H >> S) or inferior (H << S) to the width of the pedal sole. On the right side, a peripodial groove is present, from the anus to the buccal area. The anus is posterior, median, very close to the lateral side of the pedal sole. The position of the pneumostome on the hyponotum, relative to the notum margin and the lateral side of the pedal sole, varies from about 1/3 close to the pedal sole (i.e., 2/3 to the notum margin) to 1/2 close to the pedal sole (i.e., 1/2 to the notum margin). However, several individuals occasionally have a pneumostome that is 1/4 (e.g., FLMNH 245142) or 2/3 (e.g., FLMNH 245777) close to the pedal sole. The pneumostome is not median: it is close to the median line, but slightly on the right side. The position of



FIGS. 6, 7. External morphology. FIG. 6: FLMNH 245777 #1, ventral view, total length = 35 mm; FIG. 7: Same as Fig. 6, ventral view of the posterior end of the foot, with openings (anus, female aperture, and pneumostome), total width = 23 mm.

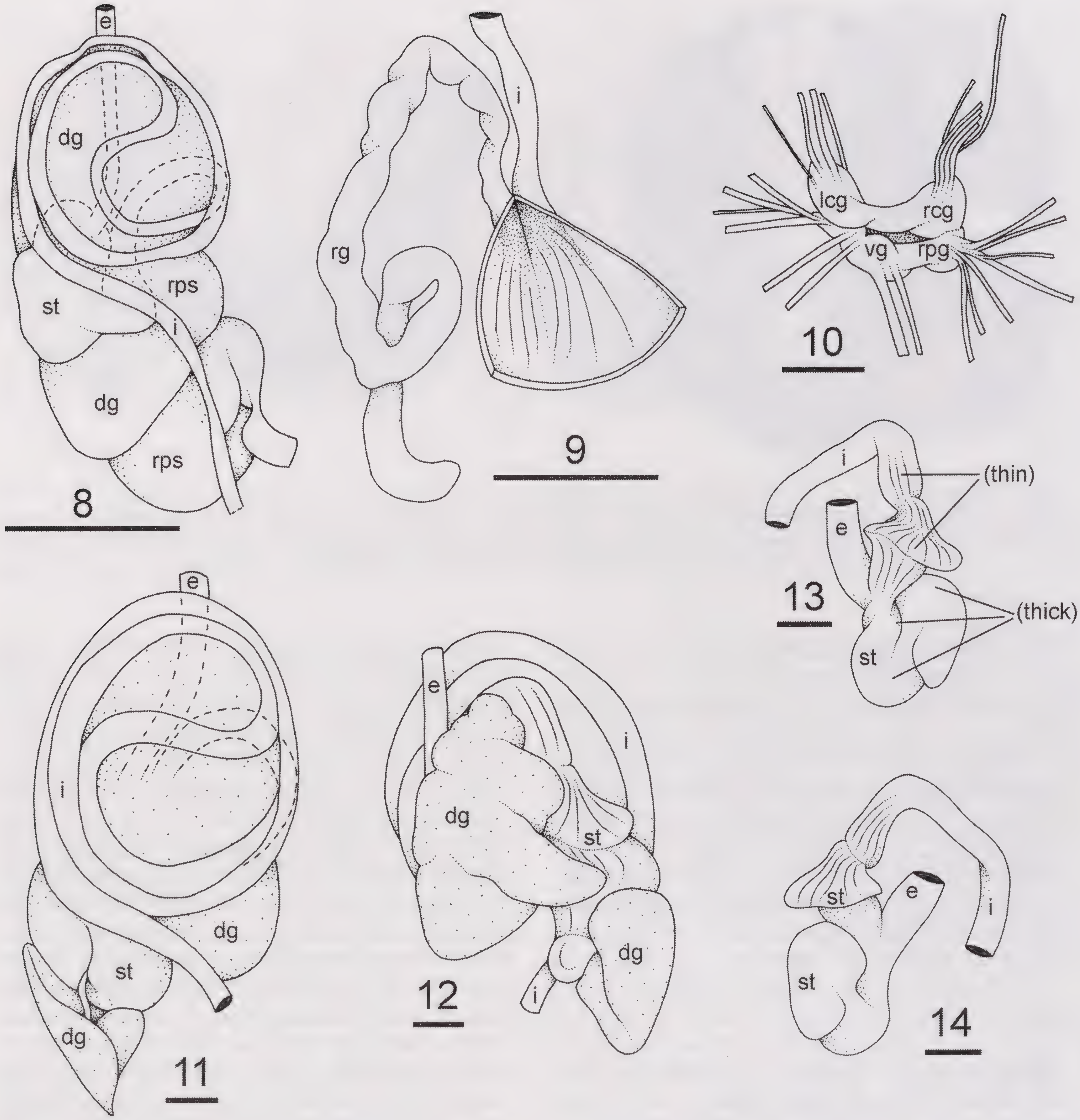
the female pore (posterior end of the peripodial groove, close to the anus) does not vary much among individuals. In the anterior region, the left and right ocular tentacles are superior to the mouth. In most preserved specimens, they are retracted inside the body. Eyes are located at the tip of the ocular tentacles. Inferior to the ocular tentacles, but superior to the mouth, the head bears a pair of oral lobes. The male aperture (opening of the penis and penial accessory gland) is located below and on the right lateral side of the right ocular tentacle.

Visceral Cavity

Marginal glands (found in *Onchidella* species) are absent. The anterior pedal gland, lying free on the floor of the visceral cavity, below the buccal mass, is oval and flattened. The visceral cavity is not pigmented internally and not divided (the heart is not separated from the visceral organs by a membrane).

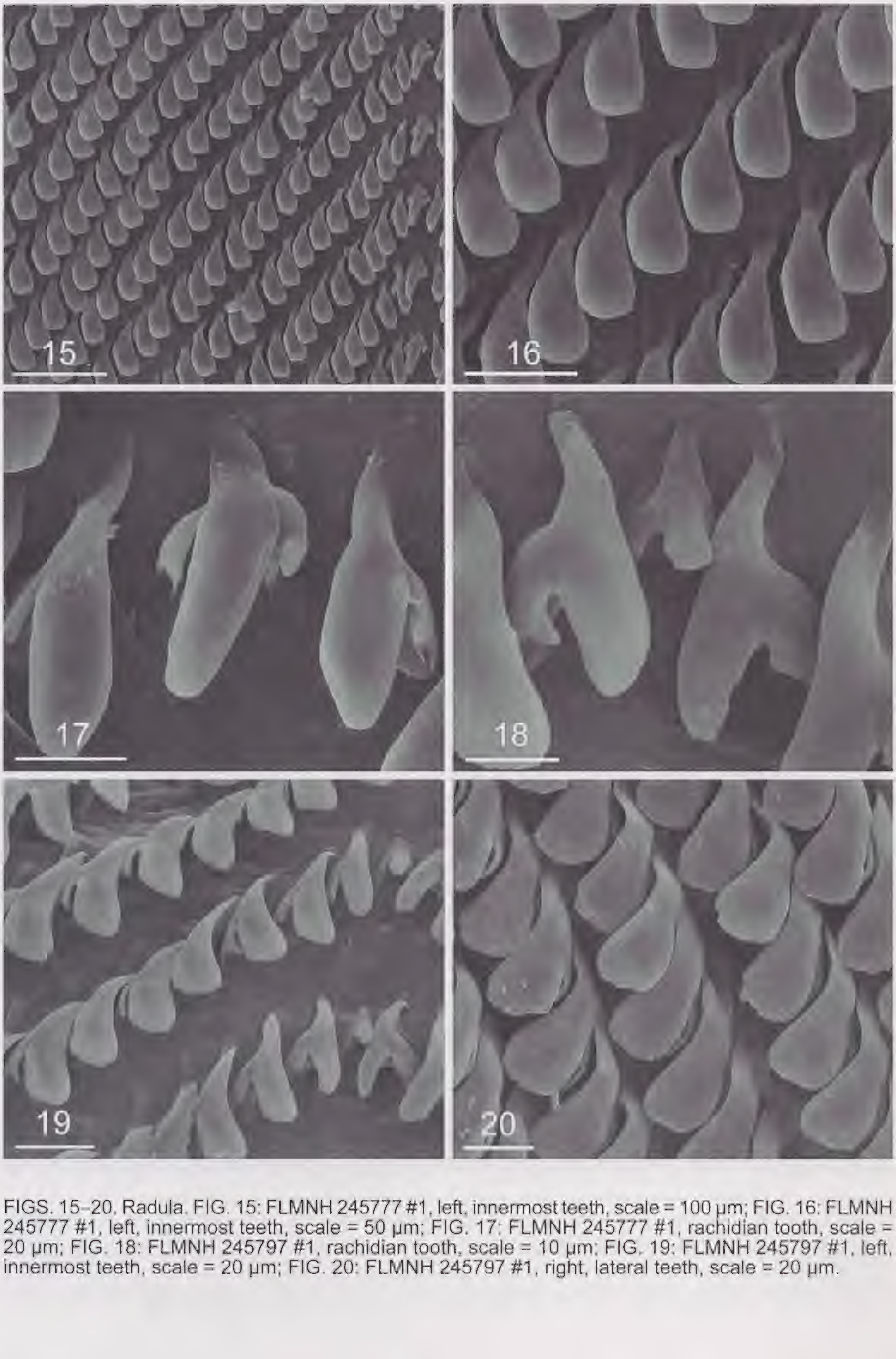
Digestive System (Figs. 8–26)

There are no jaws. The left and right salivary glands, heavily branched, join the buccal mass dorsally, on either side of the esophagus. The radula is in between two large postero-lateral muscular masses. Each radular row contains a rachidian tooth and two half rows of lateral teeth of similar size and shape. Radular formulae are: 65 × (145-1-145) in FLMNH 245191 #1 (32 mm long), 55 × (95-1-95) in FLMNH 245549 #1 (25 mm), 75 × (110-1-110) in FLMNH 245777 #1 (35 mm), 55 × (80-1-80) in FLMNH 245117 #1 (20 mm), 85 × (150-1-150) in FLMNH 245117 #2 (33 mm), 55 × (80-1-80) in FLMNH 245117 #3 (19 mm), 60 × (130-1-130) in FLMNH 245797 #2 (18 mm), 60 × (125-1-125) in FLMNH 245776 #1 (26 mm), 70 × (150-1-150) in paratype #1 of *apoikistes* (35 mm), and 70 × (135-1-135) in paratype #2 of *apoikistes* (22 mm). The rachidian tooth is tricuspid: the median cusp is always present; the two lateral cusps, located on the two lateral branches of the base of the rachidian tooth, may be absent (especially in small rachidian teeth). Rachidian teeth tend to be smaller than lateral teeth (with a length of the rachidian tooth usually not exceeding 20 μm), but exceptions are not uncommon (e.g., FLMNH 245777 #1); the size of the rachidian teeth varies within a single radula (older teeth are larger). The lateral surface of the base of the rachidian teeth is straight (neither concave nor convex). The half rows of lateral teeth form an angle of 45° with the rachidian axis. The lateral teeth seem to be simply unicuspid with a flattened and curved hook with a rounded to truncate tip (length usually < 50μm), but there also is an outer, pointed spine on the lateral expansion of the base. In most cases, the lateral spine cannot be observed on a SEM picture because it is hidden below the hook of the next lateral tooth; however, when teeth are not too close (such as in the innermost and outermost regions), the lateral spines are conspicuously prominent.

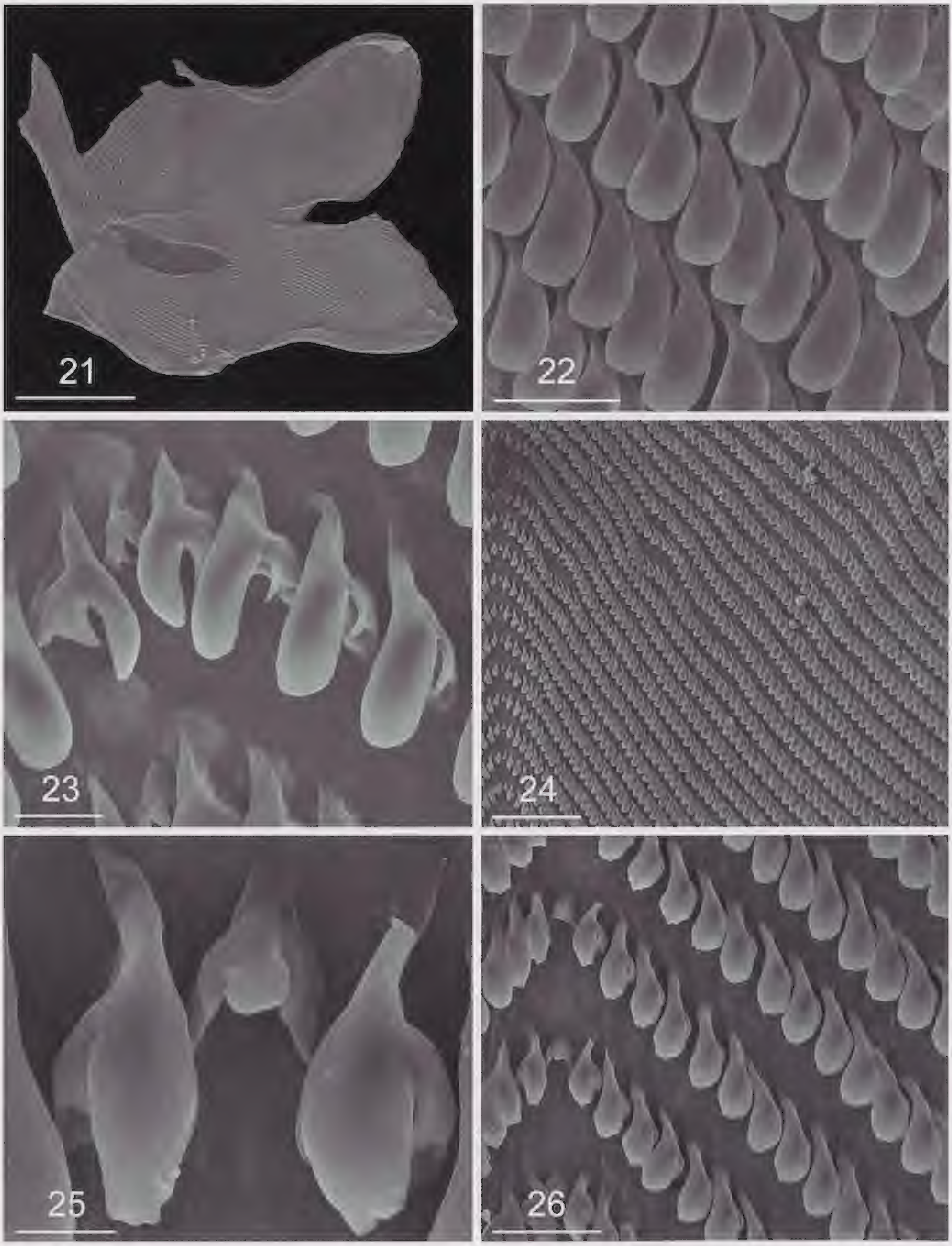


FIGS. 8–14. Digestive system and nervous system. FIG. 8: *P. apoikistes*, paratype #2, digestive system, dorsal view, scale = 5 mm; FIG. 9: *P. apoikistes*, paratype #2, rectal gland, scale = 3 mm; FIG. 10: *P. apoikistes*, paratype #2, central nervous system, dorsal view, scale = 1 mm; FIG. 11: FLMNH 245716 #4, digestive system, dorsal view, scale = 2 mm; FIG. 12: FLMNH 245716 #4, digestive system, ventral view, scale = 2 mm; FIG. 13: FLMNH 245716 #4, stomach, ventral view, scale = 2 mm; FIG. 14: FLMNH 245716 #4, stomach, dorsal view, scale = 2 mm.

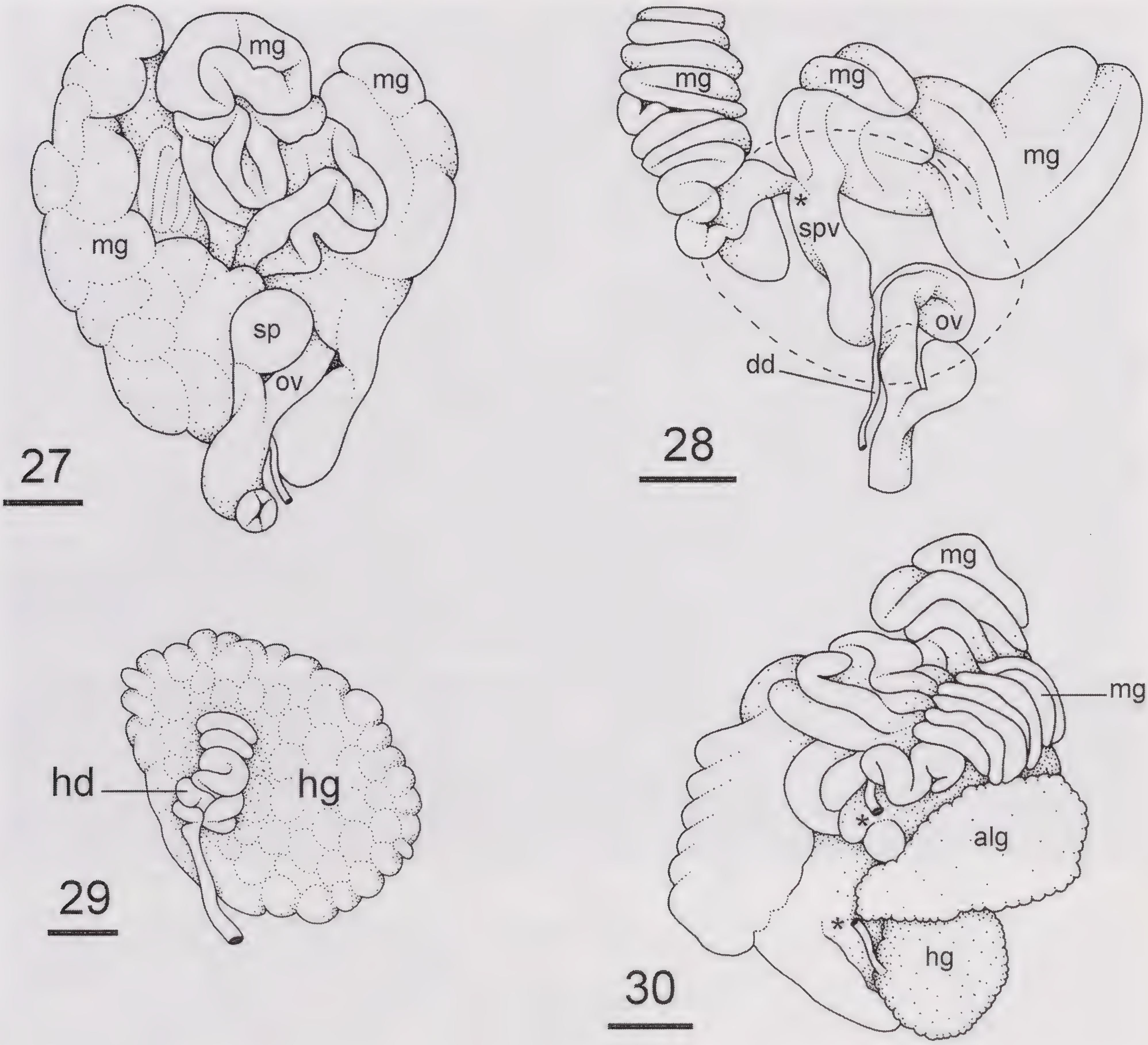
With the exception of, sometimes, the first few innermost lateral teeth, the size and shape of the lateral teeth do not vary along the half row; nor do they vary among half rows; the shape of the tip of the hook varies among individuals, from clearly truncate to clearly rounded. The esophagus is narrow and straight; its internal folds cannot be seen externally. The esophagus enters the stomach anteriorly. The stomach is located on the left dorsal side of the visceral mass and is mainly surrounded (except dorsally) by the digestive gland. It is a U-shaped sac divided internally in two compartments: the first compartment, which connects to the esophagus, is delimited by a thin layer of tissue, and the second compartment is delimited by a



FIGS. 15–20. Radula. FIG. 15: FLMNH 245777 #1, left, innermost teeth, scale = 100 µm; FIG. 16: FLMNH 245777 #1, left, innermost teeth, scale = 50 µm; FIG. 17: FLMNH 245777 #1, rachidian tooth, scale = 20 µm; FIG. 18: FLMNH 245797 #1, rachidian tooth, scale = 10 µm; FIG. 19: FLMNH 245797 #1, left, innermost teeth, scale = 20 µm; FIG. 20: FLMNH 245797 #1, right, lateral teeth, scale = 20 µm.



FIGS. 21–26. Radula. FIG. 21: *P. apoikistes*, paratype #1, radula, scale = 1 mm; FIG. 22: *P. apoikistes*, paratype #1, right, lateral teeth, scale = 50 µm; FIG. 23: *P. apoikistes*, paratype #1, rachidian and innermost lateral teeth, scale = 20 µm; FIG. 24: FLMNH 245117 #2, right lateral half rows (innermost part), scale = 200 µm; FIG. 25: FLMNH 245117 #1, rachidian and two innermost lateral teeth, scale = 10 µm; FIG. 26: FLMNH 245117 #1, rachidian and right innermost lateral teeth, scale = 50 µm.

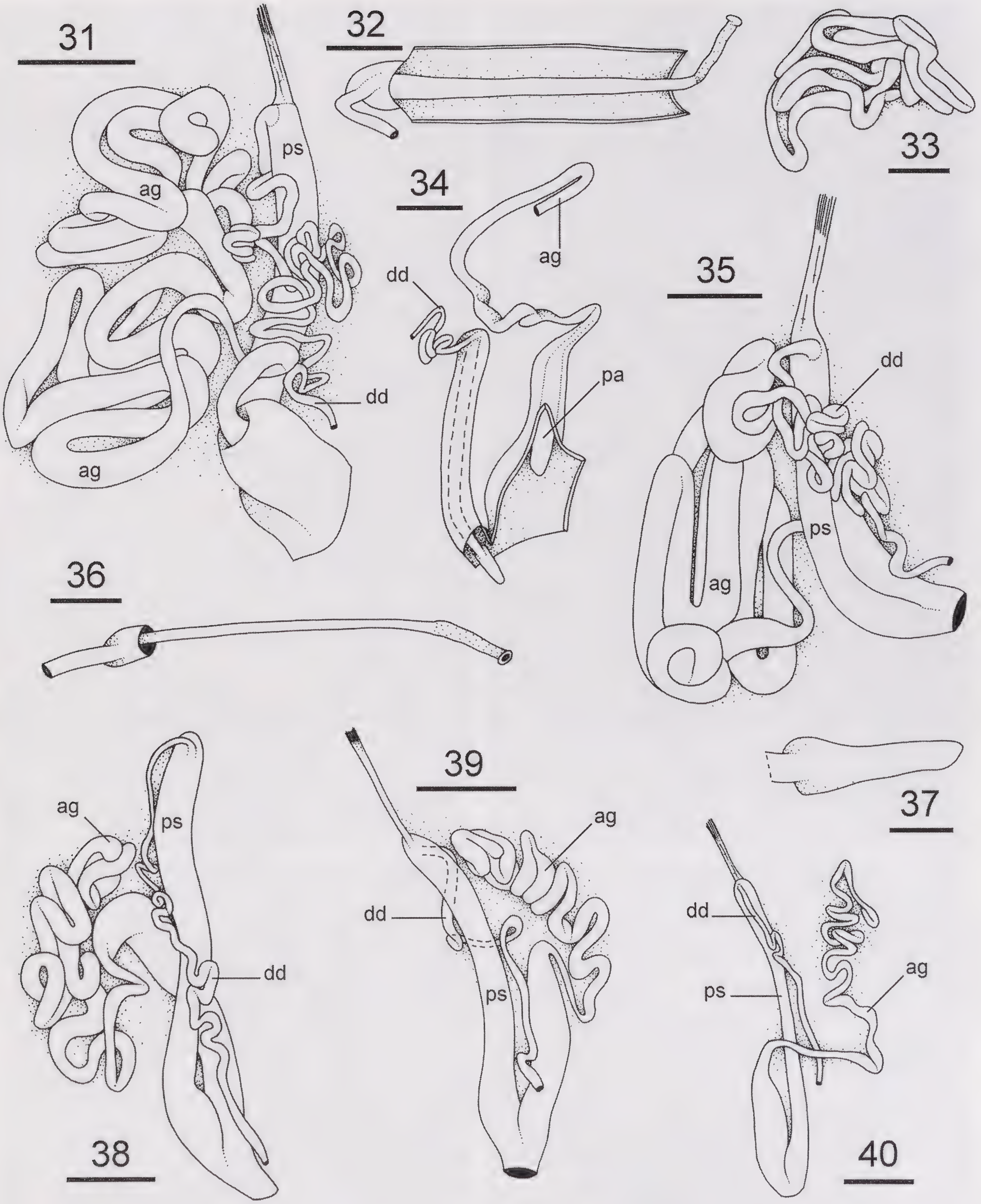


FIGS. 27–30. Reproductive system. FIG. 27: FLMNH 245716 #4, posterior part of the reproductive system, scale = 2 mm; FIG. 28: FLMNH 245716 #4, posterior part of the reproductive system (albumen gland within dotted line removed and different parts separated), asterisk indicates where hermaphroditic duct joins, scale = 3 mm; FIG. 29: FLMNH 245716 #4, hermaphroditic gland and duct, scale = 1 mm; FIG. 30: FLMNH 245716 #4, posterior part of the reproductive system, asterisks indicate where hermaphroditic duct was cut, scale = 2 mm.

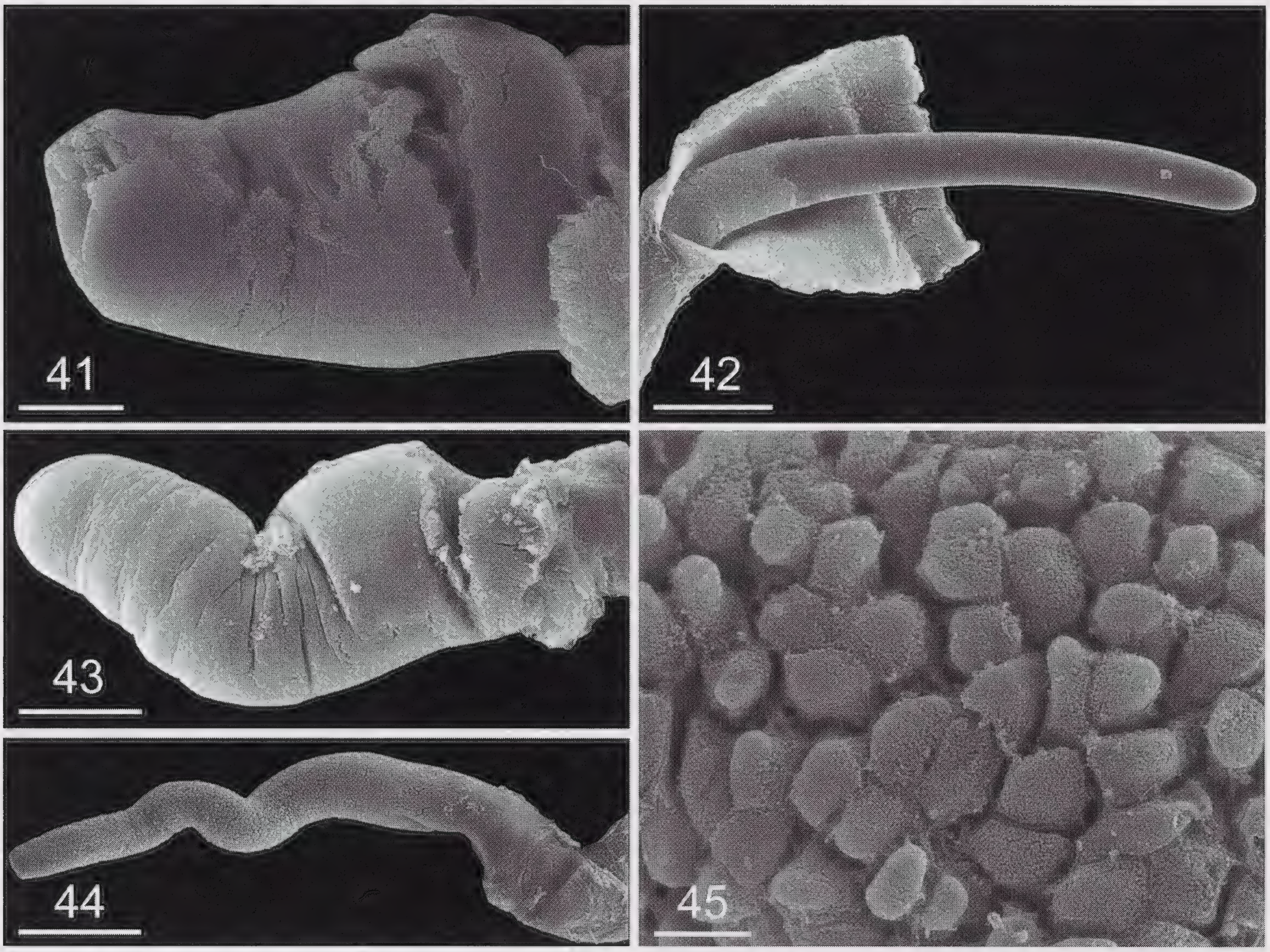
thick layer of tissue. The second compartment, externally, seems to be divided in more than one chamber, but only one chamber exists internally. No strong ridges were found on the internal surface of the stomach. The intestine is long, narrow, and of type II (characterized by two dorsal circles of the intestine), as defined by Labbé (1934). The narrow, convoluted tube of the rectal gland (unknown function) covers the postero-dorsal visceral mass and opens in the pulmonary complex, near the anus; its proximal end lies freely in the visceral cavity.

Nervous System (Fig. 10)

The circum-esophageal nerve ring is post-pharyngeal and pre-esophageal. The two cerebral ganglia are conspicuously not fused, separated by a thick cerebral commissure that is as large as each cerebral ganglion. Pleural and pedal ganglia are also distinct. The visceral commissure is very short and mainly consists of the visceral ganglion, which is on the left side of the visceral loop. Cerebro-pleural and pleuro-pedal connectives are short. In fact, pleural



FIGS. 31–40. Reproductive system. FIG. 31: *P. apoikistes*, paratype #1, male anterior parts, scale = 2 mm; FIG. 32: *P. apoikistes*, paratype #2, penis (penial sheath opened), scale = 1 mm; FIG. 33: *O. montana*, paratype #2, flagellum of male accessory gland (not represented in Tillier, 1983: Fig. 3), scale = 1 mm; FIG. 34: *O. montana*, paratype #2, male anterior parts (flagellum of accessory gland cut), scale = 1 mm; FIG. 35: FLMNH 245777 #1, male anterior parts, scale = 2 mm; FIG. 36: FLMNH 245777 #1, penis (penial sheath removed), scale = 1 mm; FIG. 37: FLMNH 245777 #1, distal papilla of male accessory gland, scale = 250 µm; FIG. 38: FLMNH 245117 #3, male anterior parts, scale = 1 mm; FIG. 39: FLMNH 245117 #1, male anterior parts, scale = 1 mm; FIG. 40: FLMNH 245797 #1, male anterior parts, scale = 1 mm.



FIGS. 41–45. Male accessory gland. FIG. 41: FLMNH 245117 #1, distal papilla (immature) of accessory gland, scale = 50 µm; FIG. 42: FLMNH 245117 #2, fully developed, hollow spine of accessory gland, scale = 200 µm; FIG. 43: FLMNH 245117 #3, distal papilla (immature) of accessory gland, scale = 100 µm; FIG. 44: FLMNH 245117 #4, distal papilla (intermediate stage) of accessory gland, scale = 250 µm; FIG. 45: FLMNH 245117 #4, same as before, surface covered with soft tissue, scale = 10 µm.

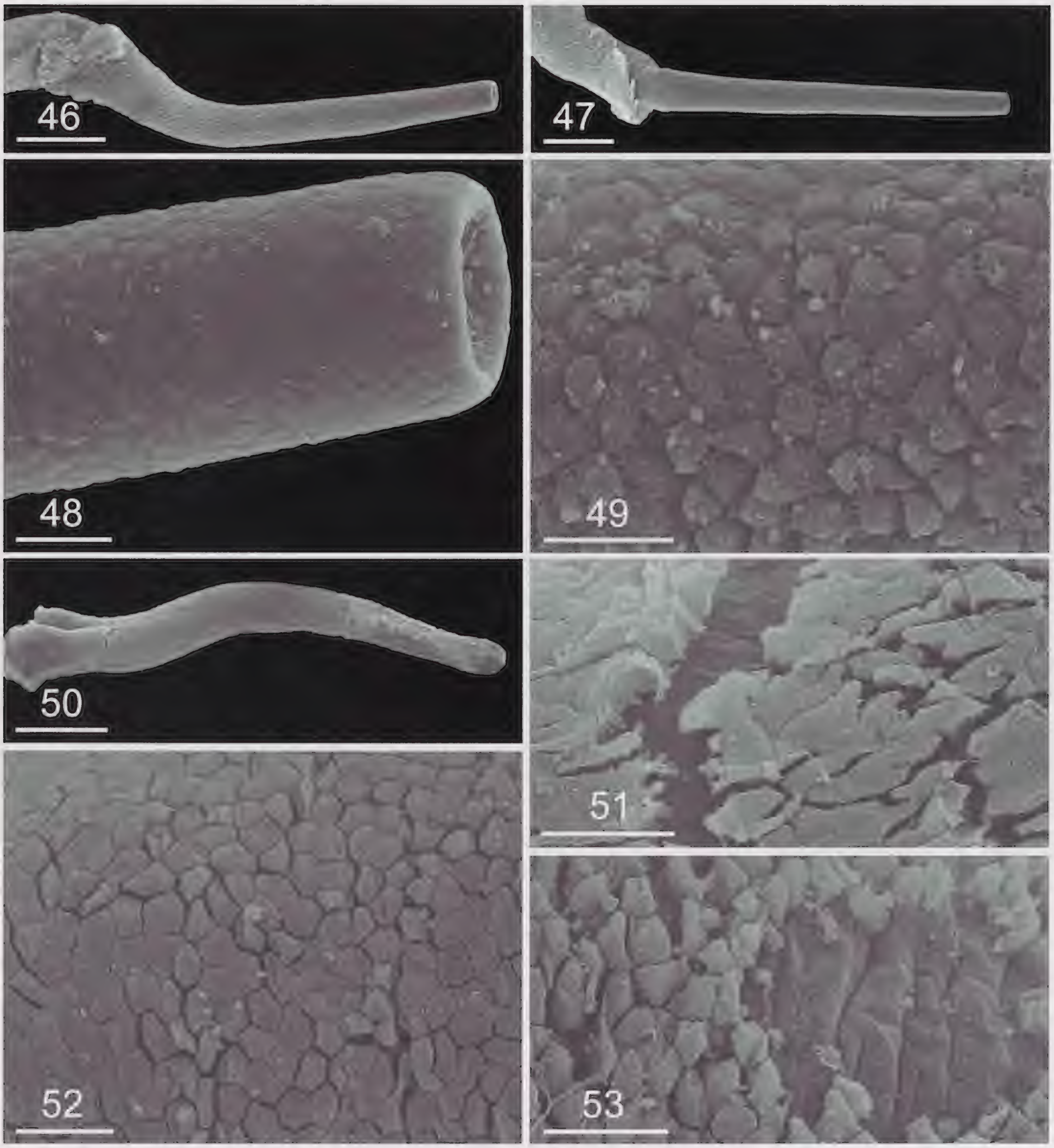
and cerebral ganglia are touching each others. Nerves from the cerebral ganglia innervate the buccal area and the ocular tentacles, and, on the right side, the male anterior organs (penial accessory gland and penial complex). Nerves from the pedal ganglia innervate the foot. Nerves from the pleural ganglia innervate the lateral and dorsal regions of the mantle. Nerves from the visceral ganglia innervate the visceral organs.

Pallial Complex

The heart is enclosed in the pericardium, located on the right side of the middle of the body cavity. The ventricle, anterior, gives an anterior vessel supporting several anterior organs, such as the buccal mass, the nervous system, and the copulatory complex. The auricle is posterior. The kidney is distinctly asymmetrical, the right part being much more developed (it runs up to the heart level) than the left part (remains posterior). The kidney is intricately attached to the respiratory complex, a lung in two left and right, asymmetrical parts.

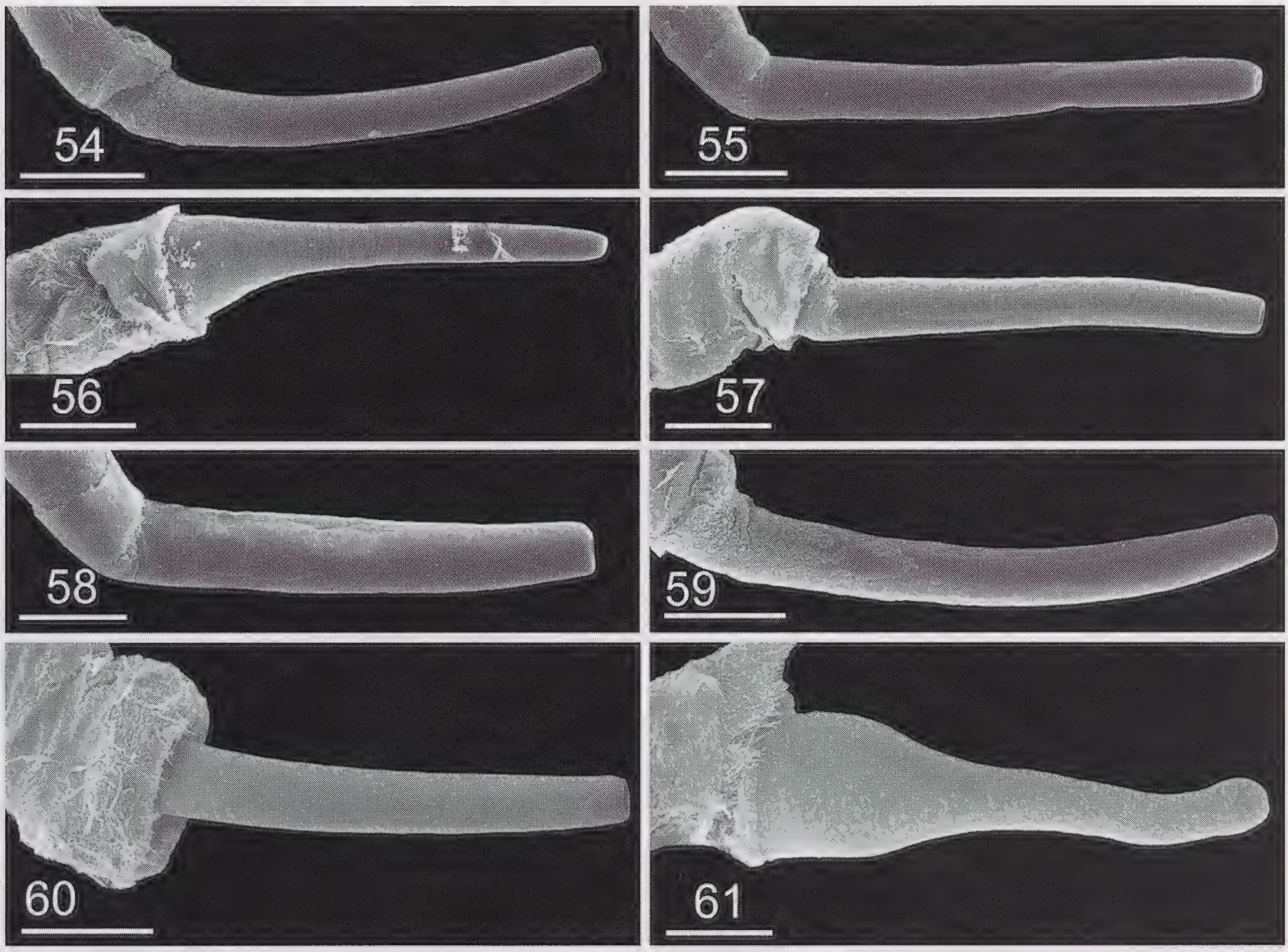
Reproductive System (Figs. 27–40)

Mature individuals have large, fully developed, female organs (e.g., large albumen and mucus glands), whereas immature individuals may have small, inconspicuous, or simply no female organs, while their anterior male parts are not fully developed either. Sexual maturity is correlated with size: all (dissected) specimens longer than 23 mm (preserved) were sexually mature; 23 mm-long specimens may be mature (*apoikistes* paratype #2; FLMNH 245776 #2) or not (FLMNH 245117 #5); all specimens < 23 mm were immature, with the exception a few specimens from Panay Island (FLMNH 245797



FIGS. 46–53. Male accessory gland. FIG. 46: FLMNH 245191 #1, fully developed, hollow spine of accessory gland, scale = 250 µm; FIG. 47: FLMNH 245191 #2, fully developed, hollow spine of accessory gland (but surface still covered with soft tissue), scale = 200 µm; FIG. 48: FLMNH 245191 #2, hollow spine tip, scale = 25 µm; FIG. 49: FLMNH 245191 #2, hollow spine still covered with soft tissue, scale = 25 µm; FIG. 50: FLMNH 245191 #3, fully developed, hollow spine of accessory gland (surface still covered with soft tissue), scale = 250 µm; FIG. 51: FLMNH 245191 #3, surface of spine still covered with soft tissue, scale = 20 µm; FIG. 52: FLMNH 245191 #3, surface of spine still covered with soft tissue, scale = 20 µm; FIG. 53: FLMNH 245191 #3, surface of spine still covered with soft tissue, scale = 20 µm.

#2, #4, and #5, 18 mm, 16 mm, and 17 mm long, respectively), but those specimens are more conical than flattened, and were alive probably much longer. The hermaphroditic gland is a single mass, joining to the spermoviduct through the hermaphroditic duct (conveys eggs and the autosperm). There is no vesicula seminalis (caecum) along the hermaphroditic

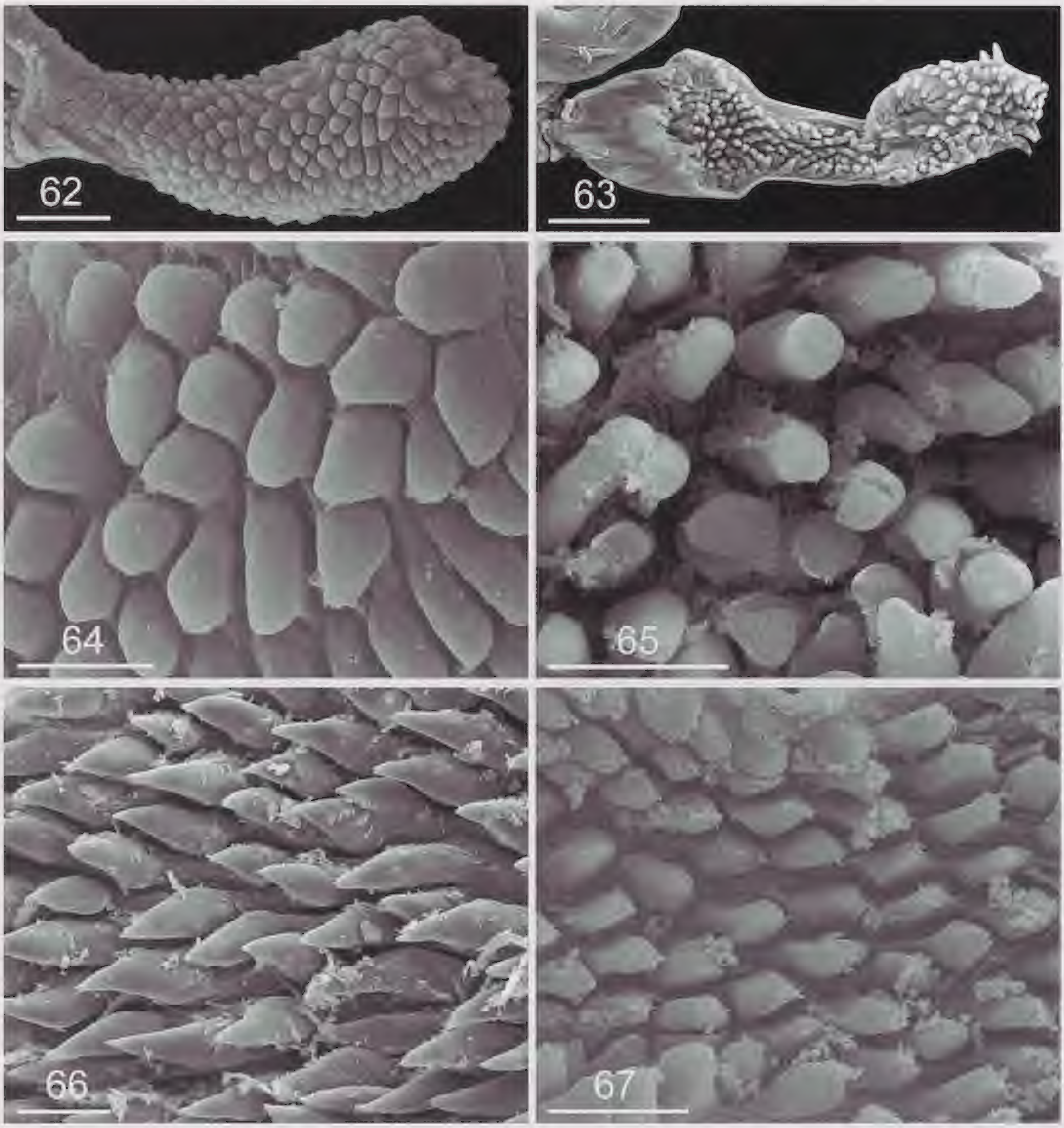


FIGS. 54–61. Male accessory gland. FIG. 54: *P. apoikistes*, paratype #1, fully developed, hollow spine of accessory gland, scale = 250 µm; FIG. 55: *P. apoikistes*, paratype #2, fully developed, hollow spine of accessory gland, scale = 200 µm; FIG. 56: FLMNH 245549 #1, fully developed, hollow spine of accessory gland, scale = 200 µm; FIG. 57: FLMNH 245776 #1, fully developed, hollow spine of accessory gland, scale = 200 µm; FIG. 58: FLMNH 245777 #1, fully developed, hollow spine of accessory gland, scale = 150 µm; FIG. 59: FLMNH 245777 #2, fully developed, hollow spine of accessory gland, scale = 200 µm; FIG. 60: FLMNH 245797 #2, fully developed, hollow spine of accessory gland, scale = 200 µm; FIG. 61: FLMNH 245797 #3, distal papilla (immature) of accessory gland, scale = 150 µm.

duct. Two highly convoluted mucous glands open where the hermaphroditic duct becomes the spermoviduct (conveys eggs, exosperm, and autosperm). For its first proximal half, the spermoviduct is not divided, at least externally. The prostate, not distinct externally, may be located within the walls of the spermoviduct. The spermoviduct is completely embedded within the albumen gland (which also covers part of the mucous glands). The opening of the albumen gland into the spermoviduct is unclear, but is likely distal to the opening of the mucous gland. Distally, the male duct becomes the vas deferens (conveys the autosperm up to the cephalic region) and is separate from the oviduct. The free oviduct (conveys the eggs up to the female opening and the exosperm from the female opening up to the fertilization chamber, near the proximal end of the spermoviduct) is about as long as the spermoviduct itself. Distally, the oviduct becomes the vagina, which is shorter than the free oviduct (about half its size). The ovate-spherical spermatheca (storage of exosperm) connects to the distal region of the oviduct through a short, wide duct.

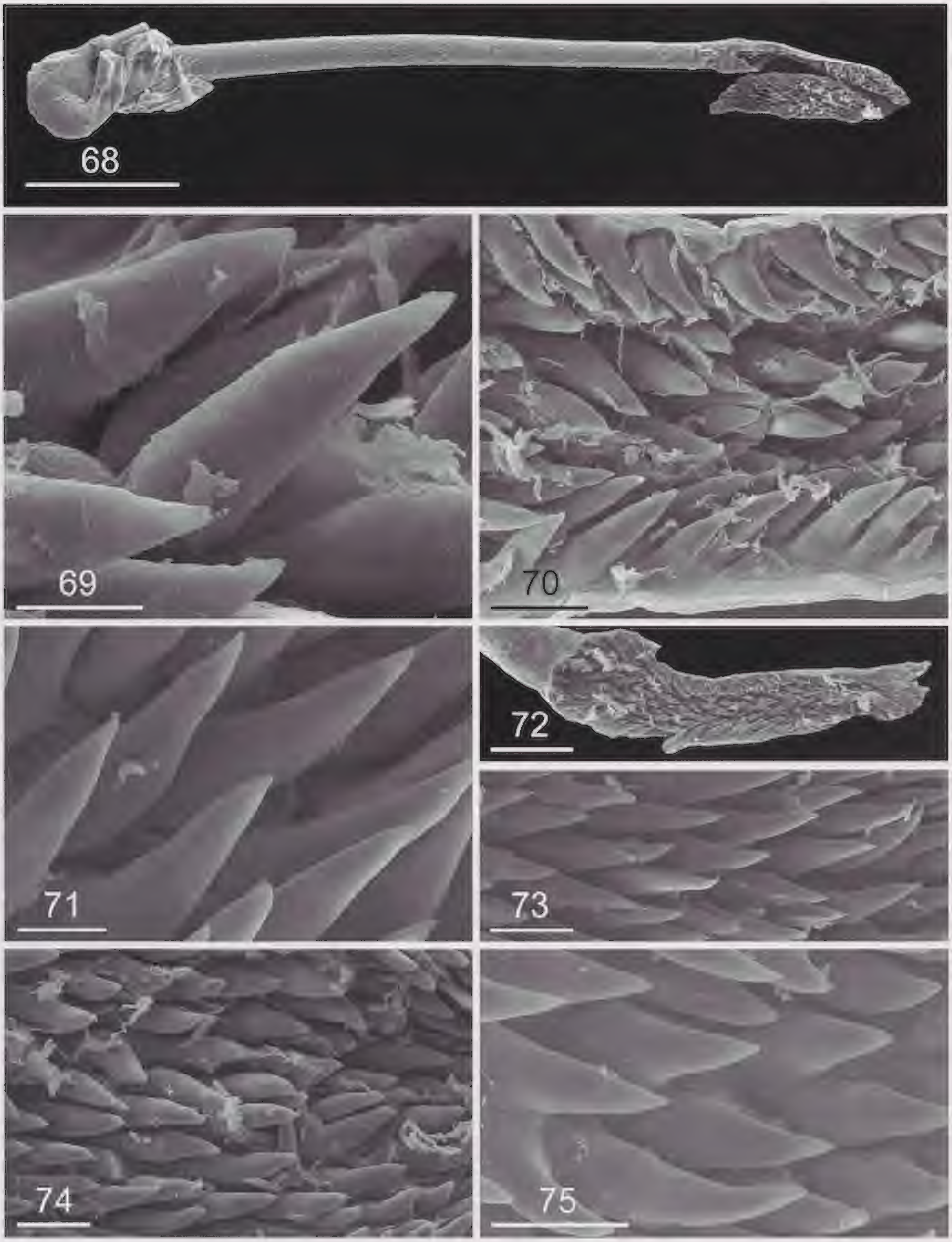
Male (Anterior) Parts (Figs. 41–75)

The male anterior organs consist of the penial complex (penis, penial sheath, deferent duct, retractor muscle) and the accessory penial gland (flagellum, papilla or spine). The penis and the penial gland share the same vestibule and the same male aperture. The internal surface of the vestibule is smooth (not covered by strong ridges or hooks).



FIGS. 62–67. Penis. FIG. 62: FLMNH 245117 #1, immature, evaginated distal end of penis (hooks not fully formed), scale = 150 µm; FIG. 63: FLMNH 245117 #5, immature distal end of penis (hooks not fully formed), scale = 250 µm; FIG. 64: FLMNH 245117 #1, same as Fig. 58, details, scale = 50 µm; FIG. 65: FLMNH 245117 #5, same as Fig. 59, details, scale = 50 µm; FIG. 66: FLMNH 245117 #2, hooks (fully formed) of distal end of penis, scale = 50 µm; FIG. 67: FLMNH 245797 #1, hooks (not fully formed) of distal end of penis, scale = 50 µm.

The length of the flagellum of the penial gland varies among individuals, depending on whether animals are mature or not. In mature individuals, the flagellum of the penial gland, long and heavily coiled, covers the dorsal surface of the buccal mass and is the first organ one sees in the anterior region when dissecting an animal in dorsal view. In individuals that are not mature, the flagellum is much shorter; although it is coiled, it does not cover the dorsal surface of the buccal mass. Distally, the flagellum ends into a soft papilla (in immature individuals) or a hard, hollow spine (in mature individuals). The papilla and the spine are located at exactly the same position (distal end of the penial gland) and are thus homologous structures. Both



FIGS. 68–75. Penis. FIG. 68: FLMNH 245549 #1, penis (proximal stalk and distal hooks), scale = 1 mm; FIG. 69: FLMNH 245549 #1, penial hooks, scale = 20 µm; FIG. 70: FLMNH 245776 #1, penial hooks, scale = 50 µm; FIG. 71: *P. apoikistes*, paratype #2, penial hooks, scale = 20 µm; FIG. 72: FLMNH 245776 #1, penial hooks, scale = 250 µm; FIG. 73: *P. apoikistes*, paratype #2, penial hooks, scale = 50 µm; FIG. 74: FLMNH 245777 #1, penial hooks, scale = 50 µm; FIG. 75: FLMNH 245191 #1, penial hooks, scale = 50 µm.

structures are hollow, likely to convey to the outside whatever is produced within the cells of the flagellum. During the development of male parts, the distal end of the flagellum first differentiates into a papilla, which is actually a duct (with a hole at its tip). This condition is found in all immature specimens. In most stations (e.g., FLMNH 245117), the immature specimens are shorter than 20 mm; exceptionally (FLMNH 245797), the immature specimens are shorter than 16 mm. The shape of the papilla changes ontogenetically, which is illustrated in all stations in which several immature specimens were available: at its earliest stage, it is simply conical (FLMNH 245117 #1) and measures only about 250 µm in length; then, it lengthens, becomes narrower (FLMNH 245117 #3), and reaches a maximum length of 1 mm; soft papillae are not straight for most of their development (FLMNH 245117 #4) and only become straight when in the process of becoming a hollow spine (FLMNH 245191 #3). The hollow spine of the penial gland is produced inside the papilla, which disappears when the hollow spine is fully formed; the external surface of early papillae is smooth, whereas the surface of late papillae forms cuboidal, separate masses of tissues ready to fall off (FLMNH 245117 #4) after the hollow spine is being formed (FLMNH 245191 #3, illustrates a superficial layer of tissue falling off from the smooth surface of the hollow spine); traces of superficial masses of tissue are sometimes observed on the surface of the (freshly formed) spines (FLMNH 245117 #2); fully mature spines, however, are completely smooth and bear no trace of any tissue from the papilla. Fully developed hollow spines measure from 0.7 to 1 mm in length, and about 100 µm in diameter. Their base is slightly larger and measures up to 200 µm in diameter. Also, spines are slightly bent at the base, although the angle varies among individuals but does not exceed 30° (and the way the spine is deposited on the stub may also influence our view). Both the papilla and the hollow spine are protected by a sheath that opens into the common male vestibule (in which the penial sheath opens too).

The penial sheath protects the penis located at the distal end of the deferent duct. The retractor muscle marks the separation between the penial sheath and the deferent duct. The latter is highly convoluted and coiled (many loops) in mature specimens; in immature specimens, it is much less coiled, and sometimes even only slightly coiled (FLMNH 245117 #1). The deferent duct is much narrower than the flagellum (~ 50 vs. 250 µm). Penial morphology is affected by age and sexual maturity. The penis of mature specimens consists of a proximal long, narrow, straight, and quite rigid stalk of 4 to 5 mm, followed by a distal soft tube densely covered internally by hooks of about 1 mm in length. Hooks are conical: they measure about the same length (about 80 µm) for a diameter of about 20 µm at their base. Hooks form a dense internal cover, with about 100 hooks on a surface of about 200 µm by 200 µm. Early in the penial development, soft papillae are observed instead of hooks (FLMNH 245117 #1 & 5, FLMNH 245797 #1); hooks are formed inside papillae (one hook per papilla).

DISCUSSION

Intra-Specific Variation

Color variation (of preserved specimens) is correlated with elevation gradient. Unfortunately, this correlation cannot be discussed in greater detail because the natural habitats of the populations studied here are unknown. In any case, populations with a light brown notum (preserved) live at lower elevations both in Panay (150–1,100 m) and Mindoro (400–600 m). Individuals with a dark bluish-black notum live at higher elevation in Panay (1,850 m) and Mindoro (1,200–1,550 m). The dorsal color of preserved individuals collected at 1,430 m from Panay is intermediary between light brown (150–1,100 m) and dark bluish black (1,850 m). Light brown individuals do not have a homogeneous brown back: their notum is always mottled with darker areas. All those specimens are identical anatomically, and there is no reason to distinguish two species based on dorsal color (one species with a bluish-black notum, and another with a brown dorsal notum). This result seems to confirm one of Britton's (1984: 181) statements on the use of color in onchidiids: "Unlike the situation in opisthobranchs, color is of very limited use in identifying onchidiaceans." More broadly, several studies have shown that the use of color pattern for taxonomic purposes in terrestrial slugs is problematic due to high intra-specific variation (e.g., Backeljau et al., 1996; Jordaens et al., 2006). Finally, it is important to keep in mind that the color variation discussed here is exclusively based on preserved specimens, and that the color of live animals might differ.

Several external characters merit to be commented on, as they were used for high-level classification or as species distinctive features. Labbé (1934) used the presence / absence of gills on the dorsal notum as a primary feature to separate onchidiids in Dendrobranchiatae vs. Abranchiatae. This division is likely invalid, as argued by Britton (1984). Whether the notum is smooth or granular varies a great deal, depending on preservation, and should probably not be used for distinguishing species. Another feature that has been commonly used in onchidiid taxonomy is the size of the hyponotum (H: width of left and right sides) relative to the width of the pedal sole (S). For instance, Labbé (1934) asserted that H < S in *Onchidium* and *Paraoncidium*, whereas H > S or = S in *Platevindex* (*Oncis*) and *Semperoncis* (*Semperella*). This character, however, varies among individuals when a large number of specimens is examined (91 specimens were examined here). The relative width of the hyponotum and pedal sole may also vary due to preservation. Finally, the position of the male aperture was used as a primary feature at supra-generic levels by all past authors (e.g., Hoffmann, 1928, 1929; Labbé, 1934; Starobogatov, 1976). According to Hoffmann (1928, 1929), in *Oncis* (= *Platevindex* + *Semperoncis*, according to Labbé, 1934) and *Onchidium* (= *Paraoncidium* + *Onchidium*, according to Labbé, 1934), the male aperture is below the right tentacle, on its left side (Labbé, 1934), a position that Hoffmann (1928) described as "inside" (*innen* in German); according to Britton (1984), in the same genera, the male aperture is located "in front of the right tentacle." However, in *Semperoncis montana*, the male aperture is distinctly on the right side of the right tentacle.

The shapes of the radular teeth illustrated here are likely not diagnostic of *Semperoncis montana*. Based on preliminary data obtained from dissections of other onchidiid species (author's unpublished data), radulae seem to be similar between closely related species, as in many gastropod taxa (e.g., all *Onchidella* species examined so far have similar radulae, which differ from the radulae found in *Peronia* species). However, the fact that SEM pictures of the radula of only three species have been published so far (including the species here) makes it difficult to discuss the variation of the shape of radular teeth. The radular formula varies a great deal among specimens of different sizes: the number of rows ranges from 55 to 75, and the number of teeth per half row ranges from 80 to 150. This information is congruent with other studies illustrating intra-specific radular plasticity and variation in gastropods (e.g., Bertsch, 1976; Reid & Mak, 1999; Kawamura et al., 2001), but is of high importance because differences in radular formulae have been traditionally used to distinguish onchidiid species. As for the pattern of intestine loops, used by Labbé (1934) to distinguish genera, Britton (1984) suggested that more than one intestine type could be present in the same species: all specimens dissected here have an intestine of type II. Finally, the rectal gland (only known in *Semperoncis* and *Onchidium* so far), was found in all specimens, regardless of their size.

The male anterior parts (penis and accessory gland) have been the most widely used features to distinguish species and also to delineate genera. However, as was already pointed out by Britton (1984: 180): "No detailed studies of variation have yet been carried out, and in particular, no attempt has been made to assess variation between populations of the same species." However, the present study, which illustrates ontogenetic changes of onchidiid male parts, raises at least two important points: (1) several species might have been regarded as distinct because mature specimens and immature specimens were being compared; and (2) the study of individual variation should ideally involve immature and mature specimens. The present results are congruent with other gastropod studies on ontogenetic and seasonal changes in genital features (e.g., Smith, 1966; Emberton, 1985; Marcos, 1992).

How many Species of Terrestrial Onchidiids in the Philippines?

When describing *Platevindex apoikistes*, Tillier (1983) found four differences between *montana* and *apoikistes*: (1) the pneumostome is closer to the notum border in *montana*; (2) the genital female aperture is more anterior in *montana*; (3) the notum is more circular and pedal sole proportionally wider in *montana*; (4) and, finally, the penial complex is very small, and a style and a style chamber are absent in *montana*.

The position of the pneumostome on the hyponotum, relative to the notum margin and the lateral side of the pedal sole, varies from about 1/3 to 1/2 close to the pedal sole in the three syntypes of *montana*, which is exactly what was found here in all *apoikistes* type material as well as all additional material. No difference was observed either for the position of the female aperture, located at the posterior end of the peripodial groove, close to the anus. As for the external shape, the description above includes specimens that are circular, individuals that are wider than long, and individuals that are longer than wide, so the shape of the three syntypes of *montana* fits perfectly within this variation range; the width of the pedal sole of the syntypes of *montana* also fits within the variation of the specimens described above.

The most important feature, however, certainly is the style. Re-examination of the largest syntype of *montana* revealed an important point overlooked by Labbé (1934) and Tillier (1983), that is, this syntype is sexually immature (its female organs are poorly developed). The syntypes of *montana* measure 15 and 18 mm in length, and all individuals examined for the present study measuring less than 20 mm were immature. The male anterior parts of this syntype are identical to the male parts observed in the immature individuals described above (Figs. 33, 34); in particular, the distal end of the accessory gland is a soft papilla instead of a hollow spine (style). As mentioned by Labbé (1934) and Tillier (1983), there is no "style" in the male parts of *montana*, but simply because the syntypes of *montana* are immature. The penis is fully developed and is identical to penises described above, that is, with a solid, proximal stalk, and a distal tube internally covered by minute hooks.

Hence the present study suggests that there is no reason to regard *apoikistes* as a distinct species from *montana*. Therefore, *apoikistes* is to be regarded as a junior synonym of *montana*. Thus, there is only one terrestrial onchidiid species distributed in three Philippine islands (Panay, Sibuyan, and Mindoro), from 150 to 1,850 m in elevation.

Supra-Specific Relationships

The terrestrial onchidiid species redescribed here was referred to as *Oncis montana* by Plate (1893) and Hoffmann (1928), *Semperella montana* by Labbé (1934), and *Platevindex montana* and *Platevindex apoikistes* by Tillier (1983). The specific name that has priority is *montana* Plate, 1893. The next task is to find a generic name.

Unfortunately, the supra-specific relationships within Onchidiidae are largely unclear, and the delineation of genera has remained largely arbitrary (Dayrat, 2009). The species *montana* is place here in *Semperoncis*, acknowledging that this assignment might very well change in the future. The genus *Semperoncis* was created by Starobogatov (1976), as a replacement name of *Semperella*, which Labbé (1934) created for a few species he wanted to exclude from *Platevindex* Baker, 1938 (which he referred to as *Oncis* Plate, 1893).

There are 16 nominal species available in *Platevindex*, six of which might not be valid, and three nominal species available in *Semperoncis* (Dayrat, 2009). All *Platevindex* and *Semperoncis* live in the tropical Indo-West Pacific, and all are marine, with the exception of the three terrestrial species already mentioned.

According to Labbé (1934), a penial gland is absent in *Platevindex* and present in *Semperoncis*. Also, according to Britton (1984), a rectal gland is absent in *Platevindex* and present in *Semperoncis*. For the rest of the diagnosis, *Platevindex* and *Semperoncis* are identical (Labbé, 1934; Britton, 1984): notum with no gills, hyponotum larger or as large as the pedal sole, male aperture below the right ocular tentacle, and asymmetrical kidney. However, none of those features, which are also found in several other genera, such as *Onchidium*, are diagnostic of *Platevindex* and *Semperoncis*. The supra-generic classifications of Starobogatov (1976) and Labbé (1934), although not based on phylogenetics, both suggest that *Semperoncis* and *Platevindex* are close to one another.

In constrast to Labbé (1934) and Britton (1984), Tillier (1983) thought there was no need to distinguish *Semperoncis* (*Semperella*) from *Platevindex*, because nothing was known about the infra- and inter-specific variation of the presence vs. absence of the penial gland, and thus regarded *Semperoncis* (*Semperella*) as a synonym of *Platevindex*. So, *montana* could be classified in *Platevindex sensu lato* (i.e., including species with and without penial and rectal glands) or in *Semperoncis*, a smaller genus restricted to the *Platevindex*-looking species with penial and rectal glands. Until onchidiid genera are delineated using a phylogenetic approach and a broad species sampling, the choice of a genus for *montana* will remain largely arbitrary. *Semperoncis* is selected here for *montana*, mainly because *montana* and *glabra* (type species of *Semperoncis*) do differ from *Platevindex* species by the presence of a penial gland and a male aperture on the right of the right tentacle.

Comments on other *Semperoncis* Species

Semperoncis includes two other nominal species, *S. glabra* (Semper, 1885), the type species, and *S. huberti* Labbé, 1934. Both species are poorly known. *Semperoncis glabra* might be re-described in the future when new material is available. *Semperoncis huberti* is here regarded as a *nomen dubium*.

Semper originally placed *glabra* in *Onchidium*. It was then transferred to *Oncis* by Plate (1893) where Hoffmann (1928) kept it, and transferred again to the new genus *Semperella* by Labbé (1934), a name replaced by *Semperoncis* by Starobogatov (1976), and, finally, transferred back to *Platevindex* by Tillier (1983). All those new generic assignments took place although no additional material was described.

The five syntypes of *S. glabra* could not be located. Most of Semper's onchidiid types are held by European museums (Berlin, Hamburg, London, Frankfurt), which have all been visited by the author to track onchidiid types, but the type material of *S. glabra* was not found. The type locality of *S. glabra* is "Camiguin de Luzon," a small island North of Luzon Island (~ 18°56"N, ~ 121°55"E). Its highest peak is at 790 m, but specimens were apparently not collected on land because the original description does not indicate any terrestrial origin (which is exceptional in onchidiids). In any case, *S. glabra* has always been regarded as a marine species. *S. glabra* is only known from its type locality.

Tillier (1983) referred to a jar containing marine *Platevindex glabra* at the Senckenberg Museum. Indeed, a lot of 10 specimens of *Oncis glabra* was found at this institution (SMF 256161), collected by Möllendorf in or before 1895, from Tablas bei Mindoro, a small island located in between Mindoro, Panay and Sibuyan. Those specimens are externally similar to *Semperoncis montana*. However, this lot is problematic for several reasons: (1) Tablas Island is far from the type locality; (2) more importantly, it is actually not possible to know whether those specimens were collected on land or on the sea shore. According to Ronald Janssen (pers. com.), curator at the Senckenberg Museum, it is more likely that this lot was collected on land because of Möllendorf's personal interests in land snails and slugs (in fact, Möllendorf collected the terrestrial type material of *montana* from Sibuyan). This is supported by the fact that the author of the present contribution found veronicellids in another jar containing onchidiids (identified as *Oncis sp.*) collected by Möllendorf from the "Philippines" with no more geographic or elevation data (SMF 256162). Thus, the lot SMF 256161 at the Senckenberg Museum is likely not a lot of *S. glabra*.

Semper (1885) did provide some information that could indicate that *glabra* and *montana* could, indeed, be closely related: no gills on the dorsal notum, presence of a rectal gland, penial gland with a distal spine, penis with distal hooks. However, other features seem to indicate that *glabra* and *montana* differ: a penis that measures only 2.5 mm long in *glabra* (penis up to 6 mm in length in *montana*), and a light yellowish dorsal notum (light brown mottled with dark areas in *montana*, or darker). Nevertheless, *glabra* remains poorly known (e.g., radula not described by Semper).

Semperoncis huberti was described by Labbé (1934) based on a single specimen collected from an unknown locality. The holotype could not be located and is likely lost. It is not held by the MNHN (collection visited by the author), where it should be. *Semperoncis huberti* is a poorly known species. Also, because the type locality is unknown, it is very likely that it will remain poorly known for quite some time and is regarded here as a *nomen dubium*. Labbé (1934) did not describe a rectal gland, and it is unclear whether it was just overlooked or really absent. Whether *huberti* should be classified in *Semperoncis* thus remains questionable. In any case, several features seem to indicate that *huberti* differs from both *montana* and *glabra*. The male reproductive organs include a penis similar to the penis described in *montana* and *glabra*, but its length (14 mm) is much longer than in the two other species. Also, the dorsal eyes, for the most part solitary in *montana*, are in groups of two or three in *huberti*. Re-identifying *S. huberti* will remain very difficult, if not impossible, which justifies its status as a *nomen dubium*.

Platevindex ponsonbyi Collinge, 1901, is also poorly-known. It was described based on a single specimen, and in three lines, exclusively based on its color ("dirty green dorsally with large, irregularly black spots. Hyponotum dark greenish-blue; foot-sole dirty yellow.") The holotype could not be located and is likely lost. Several lots of specimens collected from Borneo are held by museums, but they all are marine. It is impossible to decide whether *ponsonbyi* is the same species as *montana*, or a different species.

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